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THE COMPOUND EYES OF MACHILIS.[1]

FRANCES SEATON.

THIS study was made from the eyes of *Machilis variabilis*.[2] This insect is found in great numbers on the under surface of stones which lie near the water's edge at the bottom of Fall Creek gorge, Ithaca, N. Y.

During the last of June, when the first trips for collecting these insects were made, they were found to be of two different sizes; but in August only a few of the small ones were met with. Whether this difference in size corresponds to a difference in sex, or whether the larger ones were some that were hatched during the previous autumn and had survived the winter, was not ascertained.

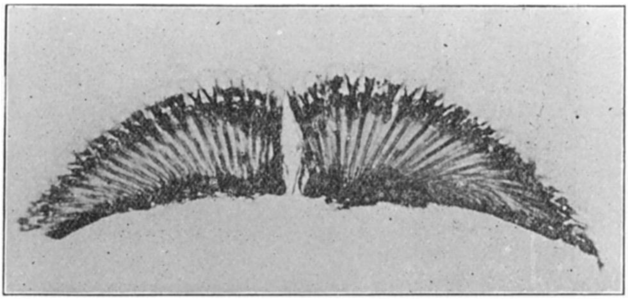

FIG. 1. A vertical section through the two compound eyes, showing their appearance before the pigment is removed.

In June and July, the exuviæ were abundant on the stones, but in August so few of these were found that it would seem as if these insects must reach the adult stage during the latter part of the summer. At this time also, the largest insects measured 1 cm. in length, excluding the antennæ and caudal filaments.

Early morning proved the best time for collecting Machilis.

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[1] Contribution from the Entomological Laboratory of Cornell University.

[2] Identified by Mr. A. D. MacGillivary.

Before ten o'clock, particularly if the mornings were damp or cloudy, they were so plentiful that as many as thirty have been captured within an hour. Toward noon as the sun neared the zenith so that its rays reached the bottom of the gorge, I have seldom found more than half a dozen specimens, and that too, in the same place where, perhaps on the following morning they have appeared as abundant as ever. This has happened so often that it has led me to believe that those creatures do not enjoy much heat and to escape it, either go farther from the surface or seek stones in a more sheltered place.

Machilis were generally found with the body, antennæ and caudal filaments lying flat against the under surface of the stone. Occasionally the posterior end of the body was raised so that the appendages of the last two and sometimes of the last three segments were raised above the ground, giving the animal an alert appearance. Unless touched, they seldom offered to move, even after the vial used in capturing them, was placed over them. They appear to be sluggish, depending upon their protective coloring as a means of escape from their enemies.

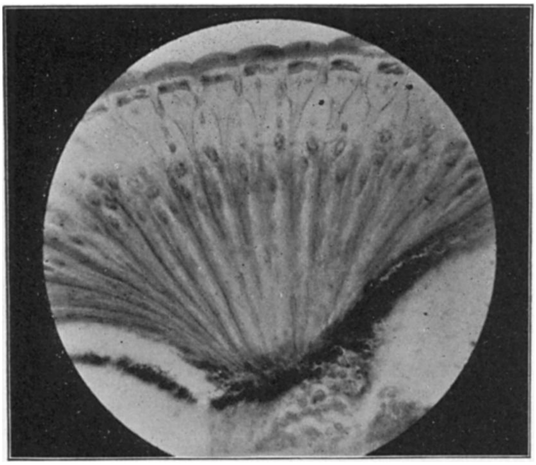

FIG. 2. A vertical section through one compound eye, depigmented and stained.

During the summer they have been kept in the laboratory in bottles containing pieces of softened, partially decayed wood upon which they have been seen feeding. Those kept in this way moulted every seven days though no one insect lived longer than three weeks.

Methods.—This study was made entirely from serial sections. Some of the sections were cut five microns thick but owing to the difficulty of obtaining such thin sections through the chitin, the greater part of the material was cut ten microns thick.

In preparing the eyes, the animals were first killed by being dropped into hot water after which the heads were placed in the fixing reagent. Before the heads were cut off, the antennæ, palpi and as much as possible of the pronotum were removed since it was found that these parts, if left on the head, interferred with the process of imbedding and cutting. The removal of these parts had to be done with great care for the pressure of the hand in holding the animal often caused a distortion of the parts of the eye thus ruining the material for study.

Of the many different fixing reagents tried the best results were obtained with Flemming's fluid, Picro-sulphuric acid, and platino-aceto formaldehyde. The eyes were cut in paraffin after which they were depigmented and stained on the slide. For removing the pigment, nitric acid, caustic potash, and peroxide of hydrogen were each tried, but the last proved to be the most satisfactory.

The stains used were Heidenhain's iron hæmatoxylin, borax carmine and Delafield's hæmatoxylin. The first was often followed by orange G. For staining nerve fibres, methelyn blue was used by injection and immersion. The method used was that given by Huber in the *Journal of Applied Microscopy*, April, '98. The results were not at all satisfactory, owing to the great amount of pigment in the eyes, which concealed all trace of the nerves. In addition to methelyn blue, Kenyon's method for the brain of the bee (*Journal of Comparative Neurology*, '96) was also tried and although this brought out beautifully the structure of the optic ganglia and the nerves proximad of the basement membrane, the eye was so uniformly stained that a definite statement as to which cells are the nerve-end cells can not be made.

The external appearance.—The two compound eyes occupy the entire cephalo-dorsal part of the head, coalescing on the epicranial suture for a distance of 2 mm. Each eye is almost circular in outline, the diameter from the anterior to the posterior margin being slightly greater than that from the dorsal to the ventral margin.

The eyes appear light green in the centre with a peripheral band of reddish brown.

The corneal cuticle. — The corneal cuticle, a transparent continuation of the body cuticle, is divided into facets which are, with a few exceptions on the periphery of the eye, uniformly hexagonal and of the same size (Fig. 3 a). Each eye contains between 450 and 525 facets. The facets have a maximum width of $23\frac{1}{2}$ microns between their parallel faces and $25\frac{2}{3}$ microns between opposite angles (Fig. 3 a).

The corneal cuticle differs somewhat in thickness in different individuals, reaching a maximum in those insects about ready to moult. The line of separation between the old and the newly formed cuticle is very distinct. This, in individuals about to moult is caused by the fact that the former is more deeply staining than the latter (Fig. 3). The maximum thickness of the cuticle at the centre of each facet is nine and one third microns, while at the periphery it is but seven microns.

The corneal hypodermis. — Proximad of the corneal cuticle and separating it from the cone-cells is the corneal hypodermis — a layer of well differentiated cells and one of considerable thickness (Fig. 3). There are two hypodermal cells beneath each facet. The distal surface of each pair of hypodermal cells is flat and hexagonal in outline (Fig. 3 b). This outline coincides exactly with that of the corresponding facet.

Extending across the distal surface of each pair of cells and perpendicular to two opposite sides of their hexagonal outline is a straight deeply staining line which marks the separation of the two cells. (Fig. 3 b). These lines are not all strictly parallel.

Proximad, the hypodermal cells become considerably smaller, having a width at their proximal end equal to that of the underlying cone which is 6 microns less than the width of the distal surface of the hypodermal cells. The proximal surface of each pair of cells is concave. (Fig. 3.)

The nuclei of the hypodermal cells are large and deeply staining. In transverse sections through the distal end of these cells

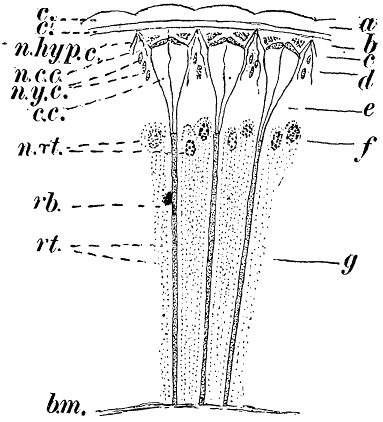

Fig. 3.

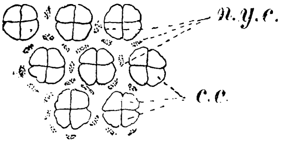

Fig. 3d.

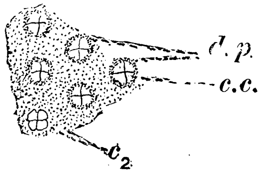

Fig. 3e.

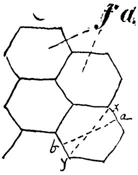

Fig. 3a.

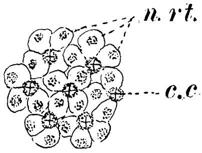

Fig. 3f.

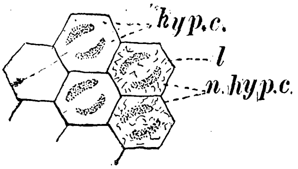

Fig. 3b.

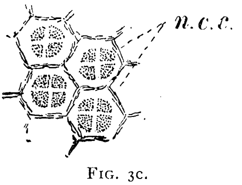

Fig. 3c.

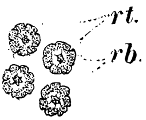

Fig. 3g.

PLATE I.

Fig. 3. A vertical section through three ommatidia of the eye of an insect about ready to moult. The ommatidia have been depigmented and stained.

Fig. 3a. A transverse section through *a,* Figure 3.

Fig. 3b. A transverse section through *b,* Figure 3.

Fig. 3c. A transverse section through *c,* Figure 3.

Fig. 3d. A transverse section through *d,* Figure 3.

Fig. 3e. A transverse section through *e,* Figure 3.

Fig. 3f. A transverse section through *f,* Figure 3.

Fig. 3g. A transverse section through *g,* Figure 3.

the nuclei are semi-elliptical, lying with their long axes parallel to the line separating the two cells. (Fig. 3 b.)

In Machilis maritima, Oudemans ('87) describes four hypodermal cells, but I am sure that there are but two in Machilis variabilis. As Oudemans figures only a longitudinal section of the ommatidia, it may be that he has made an error in observation on this point, for in such a section, two cells present the same appearance as four.

The cone-cells. — In each ommatidium, proximad of the two hypodermal cells, lie four long cone-cells (Fig. 3, *c. c.*) These cells are in close contact along their entire axial surface, forming a cone forty-five microns long with a diameter of seventeen microns at its base or distal end.

At its proximal end the cone is about two and one third microns wide. Although these four cone-cells are closely applied along their axial surfaces, yet their intercellular walls are distinct in all transverse sections of the cone from its base to its proximal end (Fig. 3 d and 3 e).

At the extreme distal end of the cone, lie the granular and deeply staining nuclei of its four cells, (Fig. 3, *n. c. c.*) In transverse sections through these nuclei, each is seen to have the same triangular form and size as that of the cells to which it belongs, thus entirely filling its distal end. (Fig. 3 c.) In longitudinal sections, these cone-cell nuclei appear to have their greatest thickness over the centre of the cone and gradually diminish in thickness toward the periphery. (Fig. 3, *n. c. c.*)

The convex distal surface of these cone-cell nuclei fits into the depression on the proximal surface of the two hypodermal cells. (Fig. 3.)

Whatever the substance of the cone cells may be, it is but slightly affected by dyes. In most preparations it appears absolutely unaffected by them, remaining a perfectly hyaline structure.

The distal pigment.—Surrounding the posterior two thirds of each cone, is a sheath of pigment which appears black in masses, but whose separate large round granules are maroon in color. (Figs. 3 e, and 7.) Outside of this thin sheath of black pigment and separating the cones of the different ommatidia, is a brownish yellow pigment. The cells containing this last pigment extend from a short distance distad of the proximal end of the cones up between the cones and hypodermal cells to the corneal cuticle to which they appear to be attached. (Fig. 3.) The nuclei of these cells lie between the outer ends of the cone-cells (Fig. 3, *n. y. c.*) In a transverse section through the cone, just proximad of the cone-cell nuclei, the nuclei of these yellow pigment cells appear arranged in a circle around each cone (Fig. 3 d). As these nuclei lie at different levels in the eye, their exact number is difficult to determine. Not less than eight have been counted and in some sections, as many as ten or twelve, so that each cone is surrounded by at least three yellow cells and possibly as many as six.

It may be possible that these yellow cells constitute an iris tapetum as in the cabbage butterfly; or they may contain a pigment that acts as such, as in the Dragon fly. (Exner '91.)

In transverse sections through the proximal half of the cones, the black pigment mentioned before occupies a narrow ring around each cone from which it is separated by the peripheral cell wall. (Fig. 3 e.) Outside of this ring of black pigment and filling up the interstices between the cones, lies the brownish yellow pigment. (Fig. 3 e.) It seems probable from both transverse and longitudinal sections that the two kinds of pigment which surround each cone represent two distinct circles of cells, although no nuclei have been found in the narrow area occupied by the black pigment.

Although eyes have been examined from insects which have been kept for three hours in the dark previous to killing, as well as eyes from other insects which have been kept in the light, for an equal length of time, no change in the position of the black or "iris" (Exner) pigment was noticed.

The rhabdoms.—The rhabdoms are the long, rod-like structures which lie between the proximal ends of the cones and the basement membrane (Fig. 3). They occupy about two thirds the entire depth of the ommatidia. At its distal end each rhabdom is equal in width to the proximal end of the cone against which it presses (Figs. 2, 3, and 5). Proximad, the rhabdoms taper slightly until at the basement membrane they are only one micron in width. The rhabdoms are fluted, having in transverse sections the form of a seven-pointed star (Figs. 3 g, and 7).

In sections from which the pigment has not been removed, the rhabdoms appear as perfectly hyaline structures, while in depigmented and stained sections, with the exception of a small central core, they invariably appear non-granular and deeply staining. (Fig. 3, and 2). Thus the rhabdoms present a decided contrast to their cones which are but slightly affected by dyes, if at all.

There has been no indication in any of the sections that the rhabdoms consist of seven parts or rhabdomeres, except that in cross section they appeared as seven pointed stars. (Figs. 7 and 8.)

In many longitudinal sections they often have a peculiar beaded, or sometimes a corkscrew appearance. (Fig. 9.) This peculiarity has been noticed in sections so differently treated that, at first, it seemed as if it must be due to the presence of nerve fibres in the rhabdoms but it now seems that it is probably an artifact.

That the cones and rhabdoms are in Machilis distinct and separate structures, is evident for three reasons: — first, the rhabdoms always appear as deeply staining structures, while the cones do not; second, in transverse sections the cones appear circular in outline and divided into four parts or cells while the rhabdoms invariably have the form of a seven-pointed star; third, in longitudinal sections there is always a distinct transverse line where the cone-cells end and the rhabdoms begin. (Figs. 2 and 3.) Then, too, in many sections, the cones appear partly broken away from the rhabdoms at this point and whenever the cones were entirely separated from the rhabdoms, the break invariably occurred at this particular point. (Fig. 5.)

This is a very different condition from that which exists in the lobster's eyes as described by Parker ('90), where the four cone-cells are continued as fibers outside of the rhabdom to the basement membrane. It also differs materially from the condition found in the eyes of Mantis (Patten '86), where the cone-cells extend to the basement membrane through the centre of each ommatidium, there being no distinction between cone-cells and rhabdom.

The retinulæ.— In specimens which have not been depigmented the rhabdoms are surrounded throughout their entire length, by a thin sheath of reddish brown pigment. (Fig. 9.) In cross sections, this pigment is seen to extend up close to each rhabdom, filling the spaces between its seven points (Fig. 8.) In longitudinal sections this narrow area of reddish brown pigment surrounding the rhabdoms, appears of the same width, and as if it might be continuous with the thin sheath of black distal pigment which surrounds the cone-cells. (Fig. 7.)

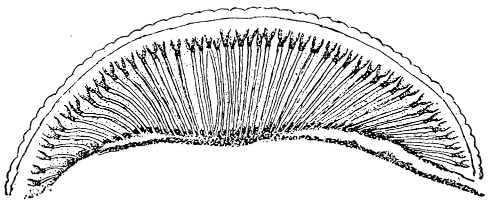

FIG. 4. A vertical section through the two compound eyes before pigment was removed; camera lucida drawing.

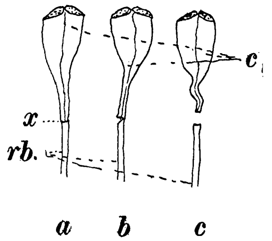

FIG. 5. A vertical section the cones and rhabdomes of three adjacent ommatidia; a, cone and rhabdom in close connection at the point *x*; b, cone partly separated from the rhabdom; c, cone and rhabdom entirely separated. camera lucida drawing.

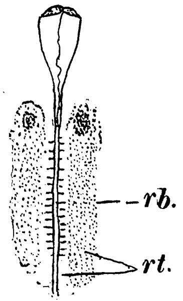

FIG. 6. A vertical section through an ommatidium which has been depigmented and stained, showing the fine horizontal lines which cross the narrow pigmented area surrounding the rhabdom.

In transverse sections of eyes that have been depigmented and stained, the narrow area immediately surrounding the rhabdom, which was before filled with pigment, now appears as a clear non-staining area and across it extend many fine lines from the rhabdom (Fig. 7). Outside of this, the area which before was faintly granular, now appears as a granular, deeply staining area whose outer edge is divided into seven distinct parts. (Figs. 3 g and 7.) Thus in transverse sections through the proximal half of the eyes, the ommatidia appear as many rosette-like figures which lie so close together that there can be little space between them in eyes. (Fig. 3 g). Each rosette-like figure has in its centre the star-like, deeply staining rhabdom which is surrounded by a narrow hyaline area. Outside of the latter is the deeply-staining granular area whose outer margin shows a distinct division into seven parts. (Fig. 7.)

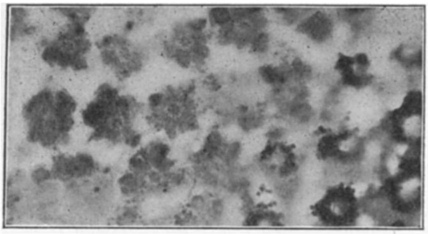

FIG. 7. A transverse section, showing the rosette-like appearance of the rhabdomes and retinulæ, depigmented and stained.

In many longitudinal sections of depigmented and stained eyes, the narrow hyaline area surrounding the rhabdoms, can be seen with a high power, to be crossed at regular intervals by many very fine lines. (Fig. 6.)

Whether the two areas surrounding each rhabdom represent two distinct circles of cells, the inner — the retinulae proper — and the outer,— accessory cells, — or whether these two areas are two parts of a single whorl of cells is difficult to determine. It seems probable, however, that since no nuclei have been seen in the inner area, we have in each ommatidium a single whorl of seven cells, the retinulæ, surrounding each rhabdom. These seven retinulæ are of uniform size and have the pigment massed on their axial border. The number of retinulæ differs from that in Machilis maritima, where Oudemans ('87) described six.

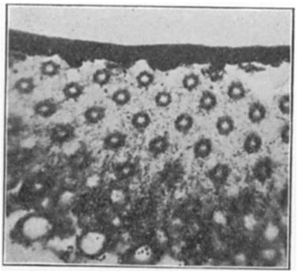

FIG. 8. A transverse section through the eye showing the rhabdomes and pigment.

In longitudinal sections of the ommatidia, the seven retinulæ are seen to extend slightly distad of the proximal end of the cone-cells, where each is considerably enlarged to accommodate its large nucleus. (Fig. 3.) The nuclei of the retinulæ do not all lie in the same plane. (Fig. 2.)

In addition to the pigment along the axial border of the retinulæ each contains considerable pigment in its proximal end so that in longitudinal sections of the eyes, this appears as a narrow band of pigment distad of the basement membrane. (Fig. 1.)

Since there is in Machilis no shifting of the iris pigment and since the rhabdoms are of uniform width, the insect, has according to Exner ('91) day eyes with apposed images.

The nerves.— Proximad of the basement membrane, lying between it and the nerve cell sheath of the optic ganglia, is a narrow area containing hundreds of minute nerve fibers which enter the eye through the basement membrane. (Fig. 9.) I am unable to say which cells of the ommatidia the nerves enter.

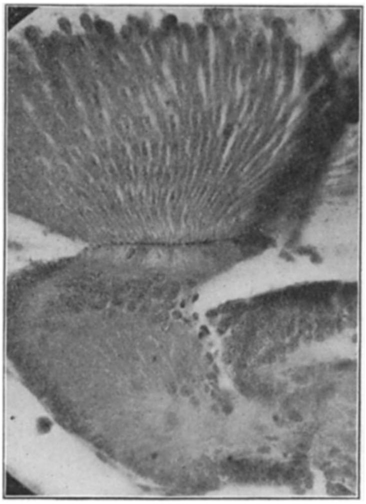

FIG. 9. A somewhat oblique section showing the narrow area proximal of the basement membrane across which the nerve fibers pass from the optis ganglia to the ommatidia.

Abbreviations employed in the figures.

c and c'.	corneal cuticle.	*n. rt.*	nuclei of retinulæ.
hyp.	corneal hypodermis.	*rb.*	rhabdom.
n. hyp. c.	nuclei of hypodermal cells.	*b. m.*	basement membrane.
c. c.	cone-cells.	*d. p.*	distal pigment.
n. c. c.	nuclei of cone-cells.	*l.*	line of separation between hypodermal cells.
n. y. c.	nuclei of yellow cells.		
rt.	retinulæ.	*fa.*	facets.